

TROPHIC ECOLOGY OF BARRELFISH (*HYPEROGLYPHE PERCIFORMIS*) IN OCEANIC
WATERS OFF SOUTHEAST FLORIDA

Barrelfish Trophic Ecology

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ABSTRACT

Deep-water demersal fishes represent an understudied but ecologically important group of organisms. Select species of demersal fishes rely on pelagic prey items, representing a direct transport of surface carbon to greater depths. Barrelfish *Hyperoglyphe perciformis* (Mitchell, 1818), which inhabit deep slope waters, are a species that has been suggested to fill this role, as congeners consume primarily pelagic gelatinous zooplankton; however, there is a dearth of information on the trophic ecology of barrelfish. Stomach content and stable isotope analyses were conducted on barrelfish caught by recreational fishers off Miami, Florida to improve our understanding of the feeding of this species. *Pyrosoma atlanticum* (Péron, 1804), a pelagic, vertically migrating tunicate, represented 89% of the barrelfish diet by weight. Mesopelagic fish and shrimp contributed much smaller proportions. Standard ellipse areas corrected for sample size (SEA_c) showed a substantially smaller isotopic niche width for barrelfish (0.606 ‰²) than dolphinfish (2.16 ‰²), king mackerel (3.04 ‰²), or wahoo (1.97 ‰²). Coupled with dependence on a singular prey item, the low SEA_c of barrelfish suggests they occupy a limited trophic niche space. Overlap of barrelfish SEA_c with dolphinfish (99.5% overlap) and king mackerel (100% overlap) indicate that the carbon sources as well as the number of trophic steps for barrelfish are similar to king mackerel and dolphinfish and are linked to surface waters. This trophic linkage suggests that barrelfish may play a role in carbon export and further study into their behavior and daily consumption rates is warranted for quantifying this role.

TEXT

Pathways of carbon export have become an increasingly important area of research with the increased input of inorganic carbon into the ocean from anthropogenic activities (Sabine et al. 2004, Riebesell et al. 2007, Siegel et al. 2014). A primary interest in these pathways is the vertical transfer of carbon fixed by primary producers in the euphotic zone to deeper regions in the ocean basin (Ducklow et al. 2001). Key steps in understanding this process involve knowing the community structure of both primary producers and primary consumers (Steinberg et al. 2000, Richardson and Jackson 2007, Laurenceau-Cornec et al. 2015, Siegel et al. 2016). While most research focuses on lower trophic levels, higher trophic levels such as fishes can play a significant role in the export and sequestration of carbon to deeper waters (Smith et al. 2009, Davison et al. 2013, Trueman et al. 2014).

Deep-water fishes are critical components of oceanic ecosystems as they are the most abundant group of fishes on earth, with recent estimates of biomass representing 10,000 million tonnes (Irigoien et al. 2014). These fishes are predominantly zooplanktivorous and often display diel vertical migrations that follow their prey items (Merrett and Roe 1974, Sutton and Hopkins 1996, Pusch et al. 2004, Catul et al. 2011). However, significant consumption of vertically migrating species can occur by demersal fishes that do not migrate but live near the bottom and feed in the midwater (making them more benthopelagic), thus providing a means to export carbon through consumption of vertically migrating organisms (Mauchline and Gordon 1991, Trueman et al. 2014).

An example of such benthopelagic fishes are members of the *Hyperoglyphe* genus, which are known to consume vertically migrating gelatinous zooplankton. These fishes are poorly understood with most studies focused on *Hyperoglyphe antarctica* (Carmichael, 1919), the blue-

eye trevalla, in the Indian and Pacific Oceans (Winstanley 1978, Bolch et al. 1993, Robinson et al. 2008, Fay et al. 2011). Barrelfish *Hyperoglyphe perciformis* (Mitchell, 1818) are an understudied congener present throughout the slope waters of the western central Atlantic Ocean (Filer and Sedberry 2008, Goldman and Sedberry 2011). Barrelfish, much like the blue-eye trevalla, are a demersal/benthopelagic fish that are caught at depths ranging from 200 to 400 m, grow slowly, reach maturity at six years of age, and may live as long as 85 years (Filer and Sedberry 2008). The diet of barrelfish has been examined along the Charleston Bump region (off South Carolina) where they primarily consume the tunicate *Pyrosoma atlanticum* (Péron, 1804; Goldman and Sedberry 2011). These pyrosome tunicates are an example of a gelatinous zooplankter that has substantial potential as a vector for carbon export. With filtering rates of 35 l hr⁻¹, pyrosomes can graze a considerable amount of primary productivity and return it to depth (~ 400 m) during daylight hours (Andersen and Sardou 1994, Perissinotto et al. 2007). Furthermore, pyrosome tunicates have one of the highest carbon contents of gelatinous organisms, enhancing its potential as a mechanism for carbon transport (Lebrato and Jones 2009). Large concentrations of pyrosomes can occur but are very patchy in time and space (Cowper 1960, Lebrato et al. 2013). These pyrosome “falls” can contribute substantially to carbon export, as the sinking of moribund pyrosomes are often consumed by benthic organisms (Lebrato and Jones 2009). Consumption of live tunicates by barrelfish may provide a means to export carbon outside of these falls but our understanding of this mechanisms is still limited.

This study employs diet and stable isotope analysis to better understand the trophic ecology of barrelfish. The analysis of stomach content here provides improved geographic resolution to diet studies of this species, accounting for the second diet study ever completed on this species, while our analysis of the stable isotope signatures of barrelfish is the first for the

species. Stable isotope analysis was employed to compare carbon source and trophic level of barrelfish to that of epipelagic species in the same region, specifically the ubiquitous dolphinfish *Coryphaena hippurus* (Linnaeus, 1758), the oceanic wahoo *Acanthocybium solandri* (Cuvier, 1832), and the more coastal king mackerel *Scomberomorus cavalla* (Cuvier, 1829).

A total of 29 barrelfish, 46 dolphinfish, 18 king mackerel, and 14 wahoo were collected from fishers at Crandon Park Marina on Key Biscayne, Florida from November 2014 to November 2015. Each specimen was kept on ice after capture, and upon returning to shore, fork length, standard length, and sex were recorded. The gut cavity of each fish was opened and an incision was made at the base of the throat to remove the stomach and intestine from the fish. From this, the stomach was separated from the intestine through incisions made at the pyloric sphincter.

Upon returning to the lab, the stomach contents were immediately placed in 95% ethanol. Later, the stomach contents were identified to the lowest possible taxonomic unit and the mass of each item was recorded (tunicates were treated as one prey item despite being a colonial organism and often being broken into multiple pieces). These data were then used to calculate an index of relative importance (IRI) for each prey item using the formula

$$IRI = (\%N + \%W) * \%F$$

where %N represents the numerical percentage of individuals of a particular prey type in relation to the total number of prey items. %W represents the percentage by weight of a particular prey type in relation to the total weight of all prey. %F represents the percent frequency that a prey type occurred in the total number of stomachs analyzed. The percentage of total IRI for each species was then calculated:

$$\%IRI_i = \frac{100 * IRI_i}{\sum_{i=1}^n IRI_i}$$

Where i represents a particular prey type and n represents the total number of unique prey types for a predator species.

Dorsal muscle samples were also collected from fish specimens, and were stored on ice for approximately 30 minutes until they could be placed in a -20°C freezer. Samples were dried at 50°C in a drying oven for 48 hours, or until adequately dry for processing. Subsamples (1.2-1.5 mg) were then analyzed with an Isoprime isotope ratio mass spectrometer (IRMS; GV Instruments, Manchester, UK), which yielded carbon to nitrogen ratios (C:N) and the isotopic ratios for both carbon ($^{13}\text{C}:^{12}\text{C}$) and nitrogen ($^{15}\text{N}:^{14}\text{N}$) in each sample. Values reported use the δ notation (e.g. Fry 2006) and are relative to the standards PeeDee belemnite (carbon) and atmospheric nitrogen. Using the C:N values from the mass spectrometry results, a lipid correction curve was applied to each sample following Logan et al. (2008):

$$\delta^{13}\text{C corrected} = \delta^{13}\text{C} + (7.489 - (7.489 * 3.097) / (\text{C:N}))$$

Muscle isotope ratios were successfully attained from 26 barrelfish, 36 dolphinfish, 17 king mackerel, and 12 wahoo. Isotopic niche widths for each species were compared using standard ellipse areas with a sample size correction. The standard ellipse is the bivariate equivalent of standard deviation and the standard ellipse area is calculated using the variance and covariance of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, encompassing 40% of the data for each species (Batschelet 1981, Ricklefs and Nealen 1998). The area of this ellipse is then corrected through the following equation:

$$\text{SEA}_c = \text{SEA} * (n-1) / (n-2)$$

Where SEA is the standard ellipse area, SEA_c is the sample size corrected ellipse area, and n is the number of samples for a species (Jackson et al. 2011, Jackson et al. 2012). While SEA_c values allow a comparison of isotopic niche breadth, comparisons in the overlap of these ellipses

quantifies the overlap in isotopic niche space between two species (Jackson et al. 2012). Further, Bayesian inference was used to create credible intervals around the Bayesian standard ellipse areas (SEA_B). Details of this method are described in Jackson et al. (2011), but, briefly, vague normal priors are assigned to the means and an Inverse-Wishart prior is used as the covariance matrix of isotope values for each species. The isotope data are then used to form likelihood values, which are then combined with the priors to form posterior distributions (in this case the posterior estimate of the covariance matrix is simulated using the Markov Chain Monte Carlo method). From these posterior distributions, a set of 4000 estimates of the standard ellipse area are calculated to provide the mode of the Bayesian standard ellipse areas and credible intervals.

Over 90% of the barrelfish's diet IRI was attributed to a single species, *P. atlanticum* constituting 89% of the biomass of the barrelfish's diet and 47% of the diet by number (Table 1). Other organisms consumed consisted of ruby red shrimp (Solenoceridae, IRI: 1.6%) and mesopelagic fishes (Stomiidae, IRI: 2.5%; Sternoptychidae, IRI: 0.4%; Tetragonuridae, IRI: 0.1%). It is likely that some or all of the items identified as squid (IRI: 4.1%) were bait used by fishers.

Analysis of standard ellipses for each species revealed substantial differences in the SEA_c values and substantial isotopic niche overlap of barrelfish with the three epipelagic fishes studied. The SEA_c values were much lower for barrelfish (0.606 ‰^2) than dolphinfish, king mackerel, and wahoo (2.16 ‰^2 , 3.04 ‰^2 , 1.97 ‰^2 , respectively), with the isotopic niche of barrelfish occupying an area less than a third the size of each of the other species. This was bolstered by substantial differences in the SEA_B values between barrelfish and the three epipelagic species, with little difference in SEA_B among the epipelagic species (Figure 1). Further, the SEA_c for barrelfish overlapped with the epipelagic fishes, most prominently with

king mackerel, showing 100% of barrelfish's isotopic niche overlapping with that of king mackerel (Figure 2). This was closely followed by overlap with dolphinfish (99.5%) but much less overlap with wahoo (26%).

The stomach contents of barrelfish analyzed in this study suggest an obligate connection with *P. atlanticum*. The IRI value (91.2%) is also deflated by the percent number metric, which was a conservative estimate because it was not possible to determine individual pelagic tunicates in barrelfish stomachs due to the breakdown from stomach action and the pharyngeal bones of barrelfish. Goldman and Sedberry (2011) found *P. atlanticum* to have an IRI of 87% for barrelfish using similar methods of enumeration, suggesting that dependence upon *P. atlanticum* by barrelfish is not unique to the waters off southeast Florida. A congener, the blue-eye trevalla *Hyperoglyphe antarctica*, has also been shown to primarily consume pyrosomids, leading to the possibility that an obligate connection with pyrosomids may extend to other members of the *Hyperoglyphe* genus (Winstanley 1978).

The small isotopic niche of barrelfish substantiates that they are specialist consumers with a narrow range in their carbon source and trophic level. Their isotopic niche is also nearly entirely contained within the isotopic niche space of two of the epipelagic fishes, indicating that pyrosomes represent a vector of surface carbon to depth. ^{13}C is often more labile, thus $\delta^{13}\text{C}$ of particulate organic matter is often depleted during remineralization near the pycnocline and fluctuates with depth within 400 m of the surface, suggesting the $\delta^{13}\text{C}$ signature of barrelfish is a result of consuming carbon transported to depth from the euphotic zone by pyrosomids (Jeffrey et al. 1983, Drits et al. 1992, Druffel et al. 1992, Andersen and Sardou 1994, Perissinoto et al. 2007). This is further supported by the consumption of epipelagic organisms by king mackerel and dolphinfish in this study (and others) and their rather limited vertical range, rarely exceeding

200 m in the case of dolphinfish (Table 1; Finucance et al. 1990, Oxenford 1999; Oxenford and Hunte 1999, Rudershausen et al. 2010, Tripp-Valdez et al. 2010, Merten et al. 2014a, Moore 2014, Teffer et al. 2015). However, dolphinfish exhibit highly migratory behavior and king mackerel exhibit seasonal migrations in southeast Florida which may lead to the substantially broader range in $\delta^{13}\text{C}$ in these epipelagic species when compared to barrelfish (Sutter III et al. 1991, Schaefer and Fable Jr. 1994, Merten et al. 2014b, Merten et al. 2016).

Owing to the strong trophic coupling between barrelfish and *P. atlanticum*, fluctuations of *P. atlanticum* or barrelfish may affect the population of the other species. However, quantification of this coupling strength through incorporating barrelfish abundance, growth rates, rates of *P. atlanticum* consumption by barrelfish, and potential bottom up effects on barrelfish survival (manifested through changes in *P. atlanticum* growth) is necessary to determine if this interaction is excitable (oscillatory) or unstable, a result predicted by strong coupling strengths (Wootton 1997, McCann et al. 2011). Further, being a consumer of gelatinous zooplankton may have implications for carbon export, particularly with the consumption of a zooplankter known to have massive “falls” representing significant carbon export (Lebrato and Jones, 2009, Lebrato et al. 2013). While it is uncertain if there is enough top down pressure from barrelfish on *P. atlanticum* to affect *P. atlanticum* populations, this potential link warrants further study. More studies into diet seasonality and daily rations for barrelfish are also needed to estimate the biomass of *P. atlanticum* that barrelfish consume. Given the site fidelity of barrelfish to deep water structure and their presence below fast moving Gulf Stream waters, it seems unlikely that barrelfish partake in vertical migrations to the surface, resulting in the possibility that barrelfish can serve as a mode of carbon export through consumption of pyrosomes in the aphotic zone

(Goldman and Sedberry 2011). However, there is a dearth of data on the movement of barrelfish and further studies into their vertical movements are warranted.

Observations from this study that barrelfish rely largely on a single prey item bolsters the connection between the *Hyperoglyphe* genus and pyrosome tunicates, representing a form of benthic-pelagic coupling near the shelf edge. Specifically, this insight into the strong connection between a demersal fish and a vertically migrating filter feeder—and thus potential implications for carbon export—provides a basis for learning more about such interactions and their role in carbon export in shelf break waters.

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Table 1: Prey items (to family level) and diet metrics of barrelfish and dolphinfish. %F represents the frequency that a prey type occurred in the total number of stomachs analyzed. %N represents the number of items of a prey type in relation to the total number of prey items. %W represents the percentage by weight of a prey type in relation to the total weight of all prey types. %IRI represents the index of relative importance of a prey type expressed as a percentage of the sum of IRI values for all prey types. UNID = unidentifiable

Consumer Species	Prey Family	%F	%N	%W	%IRI
Barrelfish (n=29)	Pyrosomatidae (Pelagic tunicate)	85.7	47.4	89.4	91.2
	Stomiidae (Viperfishes)	23.8	13.2	0.5	2.5
	Solenoceridae	19	10.5	0.4	1.6
	Sternoptychidae (Hatchetfishes)	4.8	10.5	0.9	0.4
	Tetragonuridae (Squartetail)	4.8	5.3	0.1	0.2
	UNID Squid	23.8	13.2	8.8	4.1
Dolphinfish (n=46)	Exocoetidae (Flying fishes)	29	14	28.7	28.6
	Carangidae (Jacks)	16.1	8.1	11.5	7.3
	Clupeidae (Sardines and herrings)	16.1	8.1	8.6	6.2
	Belonidae (Needlefishes)	9.7	3.5	21.4	5.6
	Scombridae (Atl. chub mackerel)	12.9	12.8	0.9	4.1
	Nomeidae (Man-o-war fish)	3.2	10.5	4	1.1
	Hemiramphidae (Ballyhoos)	6.5	2.3	4.4	1.0
	Balistidae (Triggerfishes)	6.5	2.3	2.6	0.7
	Lobotidae (Tripletail)	3.2	1.2	3.7	0.4
	Diodontidae (Porcupinefishes)	3.2	1.2	0	0.1
	UNID Fish	51.6	31.4	5.7	44.2
	UNID Squid	3.2	1.2	8.5	0.7

FIGURE LEGENDS:

Figure 1: Density plot of Bayesian standard ellipse areas (SEA_B) for barrelfish and three epipelagic species. Black dots represent the mode of posterior distribution of SEA_B values with grey boxes presenting 50, 75, and 95% credible intervals.

Figure 2: Stable isotope values ($\delta^{13}C$ and $\delta^{15}N$) of barrelfish and three epipelagic species, along with each species' standard ellipse.



